DO MAMMALIAN NEST PREDATORS FOLLOW HUMAN SCENT TRAILS IN THE SHORTGRASS PRAIRIE?

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ABSTRACT.—Nest predation, the major cause of nest failure in passerines, has exerted a strong influence on the evolution of life history traits of birds. Because human disturbance during nest monitoring may alter predation rates, we investigated whether human scent affected the survival of artificial ground nests in shortgrass prairie. Our experiment consisted of two treatments, one in which there was no attempt to mask human scent along travel routes between artificial nests, and one in which we masked human scent with cow manure, a scent familiar to mammalian predators in the study area. We found no evidence that human scent influenced predation rates, nor that mammalian predators followed human trails between nests. We conclude that scent trails made by investigators do not result in lower nesting success of passerines of the shortgrass prairie where vegetation trampling is minimal, mammalian predators predominate, and avian predators are rare. *Received 9 Nov 1998, accepted 10 Feb. 1999.*

Predation has exerted a strong influence on the evolution of habitat selection and life history traits for many avian species (Martin 1993b). Research on a broad array of ecological topics requires estimates of avian fecundity. Because nest predation is the major cause of nest failure in passerines (Ricklefs 1969; Martin 1992, 1993a, b), researchers have frequently expressed concerns that monitoring might artificially increase predation rates (Mayfield 1975, Major 1990, Gotmark 1992).

Predators might be attracted to nests by visual cues, such as the presence of researchers, trampling of vegetation, increased activity of parent birds, and by olfactory cues. Mammalian predators are thought to follow tracks in the vegetation and to respond to human scent along the trails or at the nests (Creighton 1971, Wilson 1976, Nol and Brooks 1982, Gotmark 1992, Whelan et al. 1994). In a review paper on investigator bias, Gotmark (1992) concluded there was little or no evidence that researcher disturbance increased mammalian predation rates. Of three studies that have directly addressed whether human scent increases mammalian predation rates (Keith 1961, MacIvor et al. 1990, Whelan et al. 1994), one (Whelan et al. 1994) supported the hypothesis. Even though evidence is scant, the use of rubber boots and gloves is widely recommended to alleviate the potential problem of human scent leading to bird nests (Nol and Brooks 1982, Yahner et al.1993, Major and Kendal 1996).

Artificial bird nests have been widely used in predation studies (e.g., Gottfried and Thompson 1978, Yahner and Wright 1985, Yahner et al. 1993). Despite problems with interpretation of results (Major and Kendal 1996), they remain a useful tool for testing predation theories. We conducted an experiment using artificial ground nests in a shortgrass prairie where the primary nest predators are mammals and human presence is rare. Our objective was to test if human scent increased the rates of predation on shortgrass prairie ground nesting birds by comparing two methods of experimenter travel between nests.

The purpose of our study was to determine the most expedient technique for ongoing breeding bird studies in the shortgrass prairie. We do not intend to make inferences from this study to other ecosystems and predator communities. Because breeding systems vary in predator communities, predator behavior, exposure to human presence, vegetation structure, and nest position, many systems need to be evaluated before we can fully understand the effect of human scent on predation rates.

METHODS

We conducted this experiment in July 1997 on Pawnee National Grassland, 7 km northwest of Briggsdale, Weld County, Colorado (40° 41′ N, 104° 24′ W). The 259 ha tract of grazed shortgrass prairie is characterized by short and mid-grasses, cacti (*Opuntia sp.*),

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forbs, and patchy areas of yucca (*Yucca glauca*). Common ground nesting passerines in the vicinity include Horned Lark (*Eremophila alpestris*), Lark Bunting (*Calamospiza melancorys*), McCown's Longspur (*Calcarius mccownii*), Chestnut-collared Longspur (*Calcarius ornatus*), and Western Meadowlark (*Sturnella neglecta*). Potential predators of ground-nesting birds include thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*), deer mouse (*Peromyscus maniculatus*), northern grasshopper mouse (*Onychomys leucogaster*), coyote (*Canis latrans*), swift fox (*Vulpes velox*), raccoon (*Procyon lotor*), long-tailed weasel (*Mustela frenata*), badger (*Taxidea taxus*), striped skunk (*Mephitis mephitis*), and several snake species.

We placed 100 artificial nests along two transects established 800 m apart in similar habitat. Each transect contained 25 lines perpendicular to the transect and alternating in opposite directions at 50 m intervals so that adjacent lines were 100 m apart. Each line contained two nests; one at 100 m (Nest A) and the second at 200 m (Nest B) from the transect. From Nest B we walked an additional 100 m so that both nests on the line were treated equally. To aid in relocating nests we noted any distinguishing features around the nest and tied surveyor's tape to low-growing vegetation 10 m from each nest, a distance not associated with increased predation rates (Major and Kendal 1996).

To test if human scent trails influenced predation rates, we subjected artificial nests to two treatments. In Treatment 1 (human scent), we wore leather boots and made no attempts to mask human scent while walking between nests. In Treatment 2 (masked scent), we masked human scent with a scent familiar to potential predators in the study area by wearing rubber boots that were sprayed with a cow manure tea (fresh cow manure steeped in water, in a 1:3 mixture for at least 12 hours) at the beginning of each line. Treatment types were randomly assigned to the 50 lines (25 lines per transect); both nests on a line received the same treatment. Because we specifically wanted to determine an effect of scent trails, we wore vinyl craft gloves (standard field practice) while handling eggs in both treatments to minimize human scent on the eggs.

Nests consisted of a scrape on the ground and contained two fresh Japanese quail (*Coturnix japonica*) eggs (mean length × width, 3.3 × 2.6 cm, *n* = 20) and one clay egg (2.2 × 1.5 cm, *n* = 20). Scrapes were created using the broad end of a large wooden tongue depressor. While wearing rubber gloves we constructed clay eggs out of soft modeling compound (Sculpey 111 brand) to approximate the size of Lark Bunting eggs. Clay eggs aided in the identification of nest predators and enabled us to record predation by predators too small to handle quail eggs (i.e., small rodents; Major and Kendal 1996).

Nests were set out on 9 July 1997 and checked three days later, a time interval during which we expected 50% of the nests to survive based on preliminary results of trials using artificial nests constructed in the same manner. Although several studies used longer trial intervals, we expected that our ability to detect dif-

TABLE 1. Predation outcomes for 25 lines receiving the human scent treatment and 25 lines receiving the masked scent treatment.

| | Predation outcome (1 = depredated, 0 = survived) | | Number of lines with outcome | |
i	Nest A	Nest B	Human scent (n_i)	Masked scent (m_i)
1	0	0	6	5
2	1	0	5	8
3	0	1	9	7
4	1	1	5	5

ferences would be diminished if nearly all nests were depredated. Nests were classified as intact or disturbed based on signs of disturbance to either quail or clay eggs. Nests were considered disturbed if quail eggs were missing, broken, or moved, or if clay eggs were missing, moved, or had tooth impressions. We collected extant clay eggs for examination and identification of any diagnostic marks. We classified markings on the clay eggs as rodent, non-rodent, insect, or unknown by comparing them with known tooth impressions made from skulls in the zoology collection at Colorado State University, Fort Collins, Colorado. In the absence of other signs of disturbance, nests containing clay eggs with only insect marks were considered intact.

The data from this experiment are counts and can be arranged into an *i* × *j* contingency table (Table 1), where *i* denotes the predation outcome and *j* denotes the treatment (i.e., human or masked scent). While the cell probabilities for such tables are commonly modeled and estimated using standard loglinear models (e.g., Agresti 1990), reparameterization of the underlying multinomial model can lead to loglinear models that are difficult to construct or difficult to interpret. In this study we reparameterize the underlying multinomial model to address the following specific questions: (1) do predation probabilities differ for nests on a line because of differences in their proximity to the transect, (2) do predation probabilities for nests differ because of differences in human and masked scent treatments, and (3) is there evidence that predators followed the investigator's trail between nests on a line. Hence, instead of using a loglinear modeling approach, we derived parameter estimates and constructed hypothesis tests using classical maximum likelihood methods (e.g., Larsen and Marx 1986:261). The general procedure was to (1) construct the appropriate likelihood function for the data, (2) derive estimators and compute estimates for parameters under the model, (3) evaluate the likelihood function at the maximum likelihood parameter estimates to obtain the deviance (here we omit the term for the saturated model and define deviance as $-2 \times$ (log-likelihood), and then (4) test specific hypotheses using likelihood ratio tests for nested models (Agresti 1990:211). The models used in this study are presented in the Appendix. SAS statis-

TABLE 2. Three candidate models for estimating predation probabilities constructed using (A.1).

Model	Parameters and Constraints	Deviance
1	p_A, p_B, c_A, c_B	137.182
2	$p_A = p_B$, $c_A = c_B$	138.549
3	$p_A = p_B = c_A = c_B$	138.589

tical software (version 6.12 on an IBM-compatible microcomputer; SAS Institute Inc. 1990) was used for all computations. Values reported are means (±SE).

RESULTS

During the trial, 49 of 100 nests were disturbed, 24 from the human scent treatment and 25 from the masked scent treatment. Disturbance to quail eggs was apparent in 45 of 49 (92%) nests; eggs were missing from 12 nests, broken in an additional 7 nests, and moved in an additional 26 nests. In four nests, the quail eggs were undisturbed, yet clay eggs were either moved or had tooth impressions. Clay eggs were undisturbed in only two nests with disturbed (broken) quail eggs. Rodent tooth impressions were identified on 22 clay eggs, and non-rodent impressions on one clay egg. Clay eggs were missing from 20 nests. Quail eggs and clay eggs that were moved were displaced an average of 31.3 cm (± 9.10, median 1 cm, range 0.5–330 cm, $n = 41$) and 43.2 cm (± 15.07, median 20 cm, range 0.5–250 cm, $n = 20$) from their original positions, respectively.

Predation outcomes for the two treatments are summarized in Table 1. In general, few differences between the treatments were evident. In Table 2, the three candidate models constructed under A.1 are presented, along with their deviance. The likelihood ratio test between model 2 and model 1, which tests for differences in predation rates between nest A and nest B caused by their proximity to the transect, had a P-value of 0.505 ($\chi^2 = 1.37$, $df = 2$). Hence, there appears to be no effect as a result of proximity to the transect. The likelihood ratio test between model 3 and model 2, which tests for differences in predation rates caused by differences in the human and masked scent treatments, had a P-value of 0.841 ($\chi^2 = 0.04$, $df = 1$). Hence, we conclude there was no treatment effect.

For the two-parameter model in A.2 (i.e., p, p'), which allows unconditional and conditional predation probabilities for nests on a line to differ, we get a deviance of 97.094. When we impose the constraint $p = p'$ (giving us a one-parameter model that is equivalent to model 3 in Table 2), we get a deviance of 98.387. The likelihood ratio test for these models, which tests whether predators were following the investigator's trail between nests on a line, had a P-value of 0.256 ($\chi^2 = 1.29$, $df = 1$). Consequently, we conclude predators did not follow the investigator's trail between nests on a line.

The one parameter models from A.1 and A.2 are mathematically equivalent and, based on the likelihood ratio tests, are the appropriate models to use for parameter estimation. Hence, the estimated three-day predation probability for nests in this study was 0.49 (±0.050), which gives an estimated daily survival probability of 0.80 (±0.026).

DISCUSSION

We found no evidence that human scent trails to nests altered predation rates on artificial nests in grasslands where the main predators are small mammals, nor did we find evidence that predators were more likely to depredate nests on the same trail. A learned association of human scent with food is unlikely because human presence is rare throughout much of our study area. Rather, the scent would be novel to small mammals of the region. We found no evidence that novel scent was an attractant to predators in our region.

Whether human scent is an attractant or deterrent to predators has been a topic of speculation (Creighton 1971, Mayfield 1975, Wilson 1976, Gotmark 1992) that has been directly tested in only three other studies. Results differ between studies. Keith (1961) reported no effect of human scent on survival of artificial duck nests in wetlands with predominately mammalian predators. MacIvor and coworkers (1990) found that red fox (*Vulpes vulpes*) avoided human scent associated with experimental plover nests along a beach. In contrast, Whelan and coworkers (1994) reported raccoons in a forested system preying on nests with human scent and novel scent more frequently than nests with no scent or familiar scent. In another study evaluating the influence of familiar and novel scents, Clark

and Wobeser (1997) determined that a novel odor (lemon juice and ground ginger root) did not affect survival of artificial waterfowl nests. Collectively, these studies represent a broad variability in predator community composition, predator behavior, exposure to human presence, vegetation structure, and nest placement.

Evidence of other aspects of investigator bias on predation rates is also equivocal. Frequency of nest visits had no effect on predation rates of artificial nests in several studies (Bowen et al. 1976, Gottfried and Thompson 1978, Erikstad et al. 1982, MacIvor et al. 1990, Gotmark 1992, Mankin and Warner 1992), but did in two studies (Major 1990, Esler and Grand 1993), presumably because of vegetation trampling. In our study, we did not evaluate the effects of frequency of visitation nor vegetation trampling. In the shortgrass prairie, the one visit to artificial nests during construction resulted in minimal vegetation trampling.

One criticism of artificial nests is that they often contain only quail eggs and that small predators unable to handle the quail eggs may be under-represented (Major and Kendal 1996). We addressed this problem by considering nests disturbed when eggs were moved as well as broken or removed, and by using smaller clay eggs in addition to quail eggs. We found, however, that only two nests would have been misclassified as undisturbed if only quail eggs had been used.

We conclude that the procedures we used while visiting nests are unlikely to contribute to reduced nesting success of passerines of the shortgrass prairie where vegetation trampling is minimal, mammalian predators predominate, and avian predators are rare. Our conclusion is consistent with Gotmark (1992) who surmises that passerines are less sensitive to investigator disturbance than other groups of birds, scent having less effect than vegetation trampling, and increases in predation in response to human cues more common for avian than mammalian or reptilian predators. We recommend that investigators continue to evaluate whether human scent alters predation rates in avian breeding systems and not make inappropriate inferences across systems. Human scent studies that identify and describe the predator communities, habitat structure, and human influence will ultimately contribute to better understanding of observer bias in research.

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APPENDIX

For a particular line receiving either the human scent or the masked scent treatment, four outcomes are possible (Table 1). If we denote these outcomes by i ($i = 1, \ldots, 4$), let the probability of the i-th outcome be π_i and γ_i (respectively) for human and masked scent treatments, and let n_i and m_i (respectively) be the number of lines for which the i-th outcome was observed for human and masked scent treatments, then the probability of the observed data is the product of two multinomials:

$$C_1 \prod_{i=1}^{4} \pi_i^{n_i} C_2 \prod_{i=1}^{4} \gamma_i^{m_i}$$

where C_1 and C_2 are multinomial coefficients, $\Sigma_i \pi_i = \Sigma_i \gamma_i = 1$, and $\Sigma_i n_i = \Sigma_i m_i = 25$. Under the assumption that lines and nests on a line are independent (the latter assumption is tested below using A.2), we can reparameterize this model in terms of the probability nest A

and nest B were depredated for human scent treatments (p_A and p_B) and the probability nest A and nest B were depredated for masked scent treatments (c_A and c_B), to obtain a model with likelihood function proportional to:

$$[(1 - p_A)(1 - p_B)]^{n_1}[p_A(1 - p_B)]^{n_2}[(1 - p_A)p_B]^{n_3}$$

$$\times [p_A p_B]^{n_4}[(1 - c_A)(1 - c_B)]^{m_1}[c_A(1 - c_B)]^{m_2}$$

$$\times [(1 - c_A)c_B]^{m_3}[c_A c_B]^{m_4}. \qquad (A.1)$$

We derived estimators for p_A, p_B, c_A, and c_B using standard maximum likelihood methods (Larsen and Marx 1986:261). Differences in predation probabilities between nests A and B due to differences in proximity to the transect, and differences in predation probabilities due to differences in treatments, were tested by constraining parameters in A.1 to obtain the appropriate submodels, and then performing likelihood ratio tests. In the first submodel parameters were constrained so that, within a treatment, predation probabilities for nests A and B were constant (i.e., $p_A = p_B$ and $c_A = c_B$). In the second submodel parameters were constrained so that predation probabilities were constant between nests A and B and across treatments (i.e., $p_A = p_B = c_A = c_B$; see Table 1).

In an effort to determine whether predators were following the human trail between nests, one additional model was constructed. This model assumed that predation probabilities among nests on a line and among treatments did not differ, but allowed the unconditional and conditional predation probabilities of nests on a line to differ. Here, the conditional predation probability is the probability nest A would be depredated given nest B had already been depredated, or the converse. If we denote the unconditional predation probability by p and the conditional predation probability by p', then the probability neither nest on a line is depredated is given by $(1 - p)(1 - p)$ and the probability both nests on a line are depredated is given by pp'. To obtain the probability that only one nest on a line is depredated, we exploit the fact that the cell probabilities for a multinomial must sum to one. Hence, the probability that only one nest on a line is depredated is given by $1 - (1 - p)(1 - p) - pp'$ which, after some algebraic manipulation, yields the intuitively reasonable

$p(1 - p') + (1 - p)p$. Thus, the resulting model has likelihood function proportional to:

$$[(1 - p)(1 - p)]^{(n_1 + m_1)}[p(1 - p') + (1 - p)p]^{(n_2 + n_3 + m_2 + m_3)}[pp']^{(n_4 + m_4)} \quad (A.2)$$

where n_i and m_i ($i = 1, \ldots, 4$) are as defined above. A test for $H_0: p = p'$ versus $H_a: p \neq p'$ was constructed using a likelihood ratio test.